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Notes from the Editors

Several topics will be covered in this issues "Notes from the Editors." Any comments related to any of them should be addressed to either of the Newsletter editors (Charles Powell, 2932 Sunburst Dr., San Jose, CA 95111 USA or Terry Chatterton, 8007 Ridge Rd., Arvada, CO 80002 USA). Thanks.

First, we would like to thank everyone who has help put together this, our first volume of the Newsletter, Dr. Dale Bertram, John F. Cover, Jr., Charlie Fanzlaw, Ann L. Jesup, Ed Oshaben, Anthony P. Wisnieski, and especially Dr. Jack K. Frenkel who patiently translated the Zimmerman article which appears in this issue. Anyone interested in helping with the Newsletter either with submission of articles, photographs, etc. or to help with proof reading the Newsletter before printing please contact either Newsletter editor.

Secondly, mention should be made of the Zimmerman article which has been translated and is printed here (again thanks to Jack Frenkel and Dale Bertram). This article first appeared in Salamandra, 24, (2/3) and was reprinted in the ISSD Newsletter, 2(3). It is now translated into English so the American membership will be made aware of this important reference in dendrobatid literature.

Lastly, we are again asking for the submission of articles for the Bulletin. At the writing of this editorial (late November) we are completely out of articles! There is absolute nothing present for the next year. So now is the time for you to submit articles to help the Bulletin. The first issue of volume 4 will not appear until enough material is submitted, so get out your pens (or computers) today and start writing.

-Notice-

Dr. Jack Frenkel (10030 El Monte, Overland Park, Kansas 66207) has offered to send in a group order for Ralf Heselbaus book "Pfeilgiftfrösche." The price for this book is \$27 including postage. Anyone interested in receiving a copy send payment to Jack by the 15th of February, 1991. This is a one time offer, if you miss it your out of luck.

Announcements

-The International Herpetological Symposium, Inc. is having its summer 1991 meeting in Seattle, Washington, hosted by the Pacific Northwest Herpetological Society. At this time a call for papers is being issued to anyone interested in presenting a paper at the meeting. Anyone wishing to present a workshop on some aspect of herpetology is also invited to submit a proposal. The Chairperson for "Seattle '91" is Dr. Richard A. Ross, c/o The Institute for Herpetological Research, P. O. Box 2227, Stanford, CA 94305. Tel.: (415) 941-4595 (9am to 5pm Pacific time). Deadline for submission of abstracts/titles is January 1991.

-Bob Herrington (Dept. of Biology, Georgia Southwestern College, Americus, GA 31709) is performing a national herpetological survey to determine the status of amphibian populations in the US. Anyone interested in participating should contact him at the above address.

BEHAVIORAL SYSTEMATICS AND ZOOGEOGRAPHY OF THE FORMATION OF SPECIES GROUPS IN DART-POISON FROGS (ANURA, DENDROBATIDAE)

Helmut Zimmermann & Elke Zimmermann

[From: *Salamandra* 24(2/3) 125-160. 15 Sept 1988, with permission.
Translated by Luuc Bauer, edited by J.K. Frenkel]

ABSTRACT

The behavioral repertoire of 32 species of the family *Dendrobatidae* is described on the basis of 62 behavioral parameters. According to the similarities of homologous behavioral characteristics, 9 "species groups" are established: I *Colostethus* group, II *Epipedobates pictus* group, III *Epipedobates tricolor* group, IV *Phobobates silverstonei* group, V *Allobates femoralis* group, VI *Phyllobates terribilis* group, VII *Dendrobates leucomelas* group, VIII *Dendrobates quinquevittatus* group, IX *Dendrobates histrionicus* group.

On the basis of behavioral characteristics, species group IV (*silverstonei*) and V (*femoralis*) are placed into two new genera, *Phobobates* and *Allobates* [n.g. H. Zimmermann & E. Zimmermann, 1988]. Bioacoustic measurements and behavioral studies revealed a new species within the *D. quinquevittatus* complex, described as *Dendrobates variabilis* [sp.n. H. Zimmermann & E. Zimmermann, 1988].

The degree of similarity and divergency, as well as the direction of evolutionary differentiation into species and species groups is shown by an etho-taxonomic diagram.

Taking into account climatic conditions and geomorphological factors during the tertiary and pleistocene periods, a hypothesis is proposed on how the different species and species groups may have evolved.

Key words: *Dendrobatidae*; taxonomy; behavior; biogeography; evolution; *Dendrobates variabilis* sp. n.; *Phobobates* n. g.; *Allobates* nov. gen.; [H. Zimmermann & E. Zimmermann, 1988].

1. INTRODUCTION

Dart-poison frogs and their relatives (family *Dendrobatidae*) live in the neotropical rainforests. Because of climatic conditions they have not been encountered as fossils (Silverstone, 1975, Duellman & Trueb 1986). There is no known

research on the phylogenetic history of these frogs, which are characterized by a complex courtship and highly developed brood-care (Weygoldt 1987, Zimmermann & Zimmermann 1985). No comprehensive review of the taxonomy of the family exists.

Edwards (1974) enumerates 63 different species of the pale colored and non-toxic genus *Colostethus*, which are distinguished mainly by their dorsal and lateral color patterns and by osteological characteristics. Silverstone (1975, 1976) also uses morphological criteria to characterize the more colorful and toxic *Dendrobates* with 33 species, and *Phyllobates* with 28 species. However, Myers et. al. (1978) retained only 5 species in *Phyllobates*, restricting this genus on the basis of toxicological research - further supported by albumin analysis of Maxson & Myers (1985); they transferred the remaining 15 species to the already very large and differentiated genus *Dendrobates*. In 1987, Myers reassigned 22 former species to a new genus *Epipedobates* and 8 species to the new genus *Minyobates*.

Systematists and ethologists alike agree that one should consider for classification not solely morphological and biochemical criteria, but also behavioral characteristics (Mayr 1975, Lorenz 1978, Hennig 1982, Maxon & Myers 1985). Especially in species with external fertilization, do courtship, vocalization, brood care, and other intraspecific relationships, play an important role as mechanisms of isolation and speciation (Schneider 1986, 1974; Martin 1972, Littlejohn 1977, Immelmann 1983, Eibl-Eibesfeldt 1987). Ethological research however unto now has been conducted on only a few Dendrobatid species, and mostly of parts of their behavioral repertoire only.

Therefor we summarize all published research in this field together with the results of our not yet published observations on the behavior of 16 species. In accordance with Lorenz (1941), the species with shared characteristics form 9 'species groups' (groups of species with homologous behavioral traits) with graded degrees of similarity in behavioral characteristics. An etho-taxonomical diagram assembled on this basis can provide a first hint of the phylogenetic history of dendrobatids. Because of their morphological and behavioral criteria, it appeared necessary to separate the 'silverstonei-group IV' and 'femoralis-group V' from the genus *Epipedobates* and to accord them generic rank; for species group IV we propose *Phobobates* n.g. and for species group V, *Allobates* n.g.. Based on findings described, and considering geological, geomorphological, and zoo-geographic factors, we now postulate a first hypothesis on the origin, evolution, and distribution of Dendrobatid species and species groups.

2. MATERIALS AND METHODS

During the last fifteen years we have kept in our terraria 28 of the 32 Dendrobatid species discussed here: *Colostethus trinitatis*, *Epipedobates parvulus*, *E. pictus*, *E. pulchripectus*, *E. anthonyi*, *E. tricolor*, *E. boulengeri-espinosai* complex, *Phobobates silverstonei*, *P. trivittatus*, *P. bassleri*, *Allobates femoralis*, *Phyllobates vittatus*, *P. lugubris*, *P. terribilis*, *Dendrobates auratus*, *D. truncatus*, *D. leucomelas*, *D. tinctorius*, *D. fantasticus*, *D. reticulatus*, *D. quinquevittatus* (type 1), *D. imitator* (type 2), *D. variabilis* sp. n. (type 3), *D. pumilio*, *D. granuliferus*, *D. speciosus*, *D. histrionicus*, and *D. lehmanni*. (Taxonomy according to Edwards 1974, Silverstone 1975, 1976, Myers 1978, and this article).

The terrarium conditions have been described repeatedly (Zimmermann, E. 1983, Zimmermann H. 1974, 1978B, Zimmermann & Zimmermann 1981, 1985A) so that we need not describe them here. So far we have bred 19 species, some for up to 6 generations (Zimmermann & Zimmermann 1987A). We published articles on single species and comparisons and summaries for 12 of the 28 species we kept (Zimmermann, Zimmermann & Zimmermann 1974 - 1987). Unpublished observations on 16 other species are included here (*Colostethus trinitatis*, *Epipedobates parvulus*, *E. pictus*, *E. pulchripectus*, *E. anthonyi*, *E. boulengeri-espinosai*, *Phobobates silverstonei*, *P. trivittatus*, *Allobates femoralis*, *D. tinctorius*, *D. fantasticus*, *D. quinquevittatus* (type 1), and *D. variabilis* sp.n. (type 3), *D. pumilio*, *D. granuliferus*, and *D. speciosus*).

Furthermore, we made use of the published behavioral research on many other species: *Colostethus palmatus* (Edwards 1974, Luddecke 1974), *C. trinitatis* (Edwards 1974, Krintler 1982, Sexton 1960, Test 1962, Wells 1980a), *C. collaris* (Edwards 1974, Dole & Durant 1974, Durant & Dole 1975), *C. inguinalis* (Edwards 1974, Savage 1968, Wells 1980b), *Epipedobates parvulus* (Crump 1974, Duellman 1978, Silverstone 1976, Weygoldt 1983), *E. pictus* (Aichinger 1985, Duellman 1978, Lescure 1976, Schluter 1980, 1984, Silverstone 1976, Weygoldt 1983), *E. pulchripectus* (Silverstone 1976, Weygoldt 1983), *E. anthonyi* (Silverstone 1976), *E. tricolor* (Silverstone 1976), *E. boulengeri-espinosai* (Myers & Daly 1976, Silverstone 1976), *Phobobates silverstonei* (Luling 1971, Myers & Daly 1979, Silverstone 1976), *P. trivittatus* (Aichinger 1985, Henzl 1986, Myers & Daly 1979, Schluter 1980, Silverstone 1976), *P. bassleri* (Schulte 1981a, Silverstone 1976), *Allobates femoralis* (Aichinger 1985, Crump 1974, Duellman 1976, Hodl 1983, Lescure 1976, Meede 1980, Schluter 1980, 1984, Silverstone 1976, Weygoldt 1980a), *Phyllobates vittatus* (Broodman 1974, Oostveen 1974, Silverstone 1976), *P. lugubris* (Savage 1968, Silverstone 1976), *P. terribilis* (Myers et al 1978), *Dendrobates auratus* (Breder 1946, Dunn 1941, Myers & Daly 1976, Oeser 1932, Polder 1973-1975, Savage 1968, Senfft 1936, Silverstone 1975, Wells 1978), *D. truncatus* (Silverstone 1975), *D. leucomelas* (Polder 1973-1975, Silverstone 1975), *D. tinctorius* (Ensinck 1980,

Polder 1973-1975, Silverstone 1975, Weygoldt 1982), *D. azureus* (Hoogmoed 1969, Kneller 1982b, Polder 1973-1975, Silverstone 1975, Ziegenhagen 1984), *D. fantasticus* (Kneller 1983, Myers 1982, Silverstone 1975), *D. reticulatus* (Myers 1982, Silverstone 1975), *D. quinquevittatus* (type 1) (Aichinger 1985, Duellman 1978, Lescure & Bechter 1982, Meede 1980, Myers 1982, Silverstone 1975), *D. imitator* (type 2) (Kneller 1982b, Schulte 1986), *D. variabilis* sp. n. (type 3) (Schulte 1981b), *D. pumilio* (Bunell 1973, Duellman 1966, Graeff & Schulte 1980, Limerick 1980, McVey et al. 1981, Meyers & Daly 1976, Polder 1973-1975, Savage 1968, Weygoldt 1980b, Silverstone 1975), *D. granuliferus* (Crump 1972, Goodman 1971, Myers & Daly 1976, Silverstone 1975), *D. speciosus* (Jungfer 1985, Silverstone 1975), *D. histrionicus* (Myers & Daly 1976, Silverstone 1973, 1975), *D. lehmanni* (Myers & Daly 1976, Silverstone 1975).

Observations and analysis of behavior we document here have been carried out by protocolling sequences, by photography, drawings from nature, and with a time lapse video system (National R) with Panasonic Video Recorder 8050, a Panasonic Camera with Newvicon WV 3090 E, and a Canon Zoom lens. Vocalizations have been recorded with a Uher-Electret condensing microphone (M-614) and Uher 4200 Report stereo tape recorder; the sound intensity was measured with a Bruel & Kjaer 2233 impulse-intensity meter from a distance of 20cm (re 20 p, Newton s/m²; Peak, Fast, Linear). A computer system MC 6800 modified by A. Zimmermann (1985) for sound analysis was used to analyze frequency and periodicity by means of fast-fourier transformation. Identification of individual animals was made from photographs and drawings of dorsal patterns.

For documentation, the animals used and their developmental stages were preserved after their death, either individually, or as populations, as species or species groups.

Field observations were carried out in the Ecuadorian rainforest during the months of March and April in 1984 and 1986. We paid especial attention to the vocalization, reproductive behavior and ecological circumstances of the *Epipedobates boulengeri-espinosai* complex (22 km S. Sto. Domingo de los Colorados, 20 km W Tinalandia, 1 km W Tandapi), *Dendrobates histrionicus* (18 km W and 21 Km S Sto. Domingo de los Colorados), *Dendrobates quinquevittatus* (type 1), near Rio Pastaza, from Puyo to Palora.

3. RESULTS

3.1 Behavioral Inventory and Etho-Taxonomical Diagram.

We registered 93 behavioral parameters from 32 species of Dendrobatid

frogs and have classified these into 7 functional groups: Behavior Relative to the Environment, Agonistic Behavior, Courtship, Vocalization, Behavior relative to Egg-Laying, Behavior Relative to Clutch and Offspring, and Behavior of Tadpoles. Behavioral parameters that could be listed in two (or more) functional groups have been listed only once (Table 1 and 2). For example, impressive display (assuming upright posture, calling, raising body/inflating the body with air, walking jerkily, strutting, pushing-up with front legs, or head nodding) may be seen during both aggressive behavior and during courtship.

The behavioral features listed in tables 1 and 2 must meet the following conditions:

- The criteria of homology (Remane 1952): such characteristics must have value in lower taxa, as in species of one family (i.e. *Dendrobatidae*).
- Phyletic homology (Wickler 1965): inborn characteristic, belong to the genotype.
- Behavior possibly being induced by conditions of captivity, as far as observed and could be tested, such as feeding behavior, territoriality in terrarium, have been eliminated from our behavioral catalog.
- Avoidance of "unreliable or meaningless traits" (Mayr 1975). Errors cannot be avoided completely or excluded, especially when descriptive phrases of other authors had to be used. Therefore we avoided onomatopoeic description of calls of the frogs if not accompanied by physical characteristics or sonograms.
- Avoidance of inexact, rare, or single observations. For example, we did not use the rarely observed 'female crouching under male' in courtship of *Phyllobates vittatus* (personal observations), nor courtship with toe dance of *Colostethus collaris* (Dole & Durant 1974), nor the head-biting observed in *Phobobates silverstonei* (= *bicolor*) (Luling 1971).

In view of these conditions for the 32 species, there remained 62 phylogenetically employable characteristics as listed in tables 1 and 2, and illustrated in part in figure 1. This tabulation of "shared characteristics" gave us an idea of the 'degree of similarity of behavioral traits' and a first idea of the phylogenetic relationship













		
3	12	14
UPRIGHT POSTURE	OVERTHROWING	CLASPING DORSALLY
		
31	19	27
BODY-ANAL ANAL-ANAL-TOUCHING	LARVAE CARRIED INDIVIDUALLY	F STROKES M
		
16	38	36
DUCKING	STRUTTING	OVIPOSITION WITHOUT MALE
		
54	54 (I)	52
CEPHALIC AMPLEXUS OR MOUTING	MOUNTING	THROAT DISPLAY (M, F)

Figure 1: Representation of some typical behavioral parameters according to table 1.

among these 32 Dendrobatid species. We can now classify these into 9 character-specific groups, or species groups:

- I *Colostethus* - because we have behavioral data on only 4 species, and further differentiation was impossible, we consider this entire genus as a species group, for the present.
- II 3 species in the *pictus* group
- III 3 species in the *tricolor* group
- IV 3 species in the *silverstonei* group
- V 1 species in the *femoralis* group

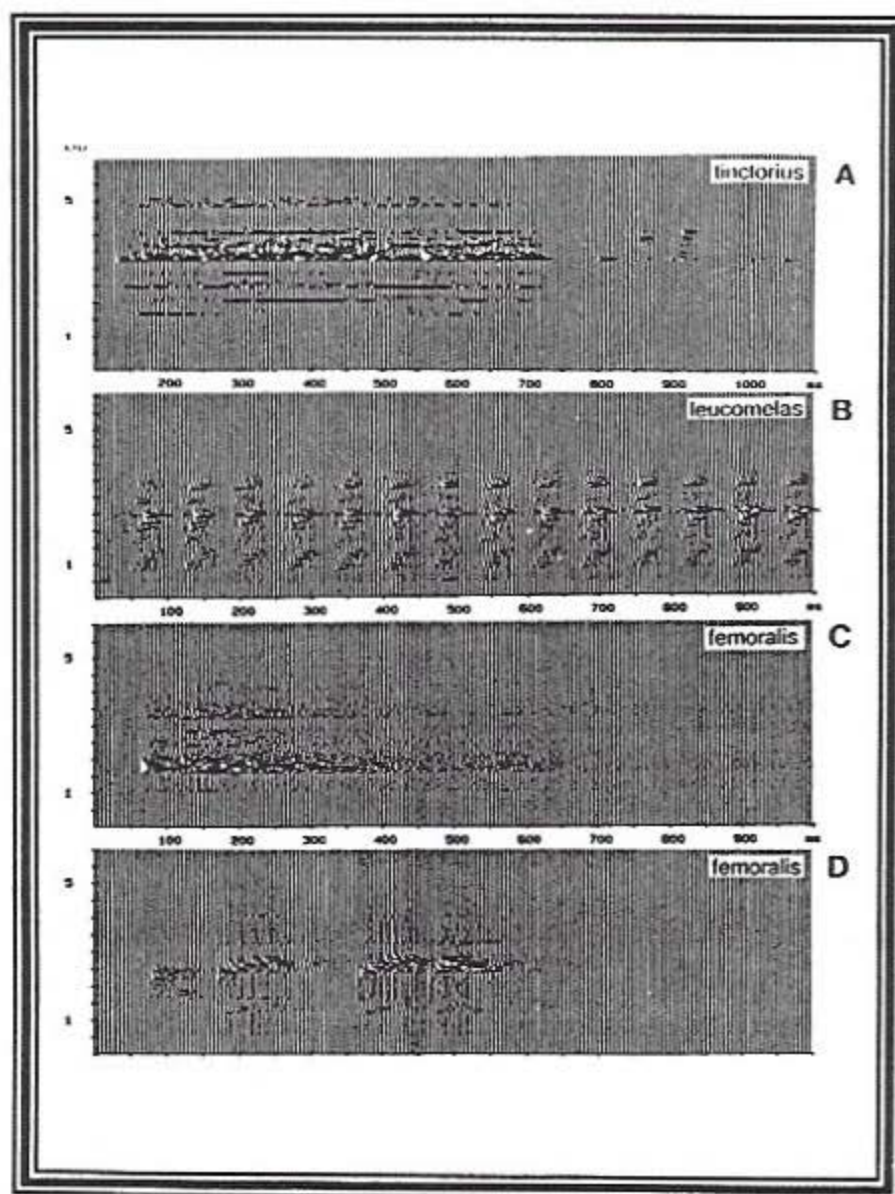


Figure 2:

Sound spectrograms
(Frequency resolution
= 25 Hz, time resolution
virtual = 5.5 ms, $t = 24^{\circ}\text{C}$.
A = Advertisement call of
Dendrobates tinctorius.
B = Advertisement call of
Dendrobates leucomelas.
C = Short range courtship
call of *Allobates femoralis*.
D = Advertisement call of
Allobates femoralis.

- VI 3 species in the *terribilis* group
- VII 5 species in the *leucomelas* group
- VIII 5 species in the *quinquevittatus* group
- IX 5 species in the *histrionicus* group

Compared to other frogs and toads, the acoustic behavior of the Dendrobatids is very complex. Not all acoustic parameters could be easily used in the taxonomic diagram (Table 2). In the *leucomelas* group, for example, there is only one call per species, either a trill or a croak. On the other hand, the *tricolor* group exhibits almost all known Dendrobatid calls from simple pulses through trills to combined calls beginning as a pulse series and ending as a croak. (Detailed acoustical analysis can be found in Zimmermann & Rahmann 1987, Zimmermann & Zimmermann 1986, 1987 and in Acoustic signals in dart-poison frogs and their implication for taxonomic and phylogenetic relationships to be published).

3.2 *Dendrobates variabilis*, a new species; [Zimmermann & Zimmermann, 1988]

The animals discussed as *Dendrobates quinquevittatus* by Silverstone (1975) we consider as 3 separate species: *Dendrobates quinquevittatus* (form 1), *Dendrobates imitator* (form 2), and *Dendrobates variabilis* (form 3). According to Schulte (1986, form 2 (*D. imitator*, or 'green two-pointer'), and form 3 (*D. variabilis*, or 'green one-pointer'), occur sympatrically, without hybridization, in the Department of San Martín, Peru. Also we did not observe any interbreeding of animals from this area in our terraria. By adding the physical call characteristics to the morphologic and behavioral characters, we define taxonomic species characteristics, as was done for primates (Zimmermann et al. 1989) and also for frogs (Schneider 1968, 1974). More detailed information especially on diagnosis will appear in a subsequent publication (Zimmermann & Zimmermann, in preparation).

In the interest of protecting animals and species, we considered preserving the still living and reproducing 'paratypes' irresponsible; However, after their death they will be given to the Staatliches Museum für Naturkunde, Stuttgart (SMNS).

Dendrobates variabilis [n. sp. Zimmermann & Zimmermann 1988.]

Holotype: No. 7054 SMNS; type locality Departamento San Martin, Peru, collected by R. Schulte in 1983.

Paratypes: living, in collection of the authors; same data as of holotype (Figure 3).

Etymology: 'variabilis' refers to the great variety in form, size, and number of spots.



Figure 3: *Dendrobates variabilis* sp. n., Paratype, Peru

Definition: Very small *Dendrobates* with snout-vent length of 15.5 - 17.8 mm; females larger than males. Back and sides bright green to yellow with rounded and often confluent black spots. One round spot on the head over the nose. Throat light green with a few black dots, belly bluish-green with many black dots. Front and hind legs green with small black spots. Length of first toe of hind leg is variable, from barely

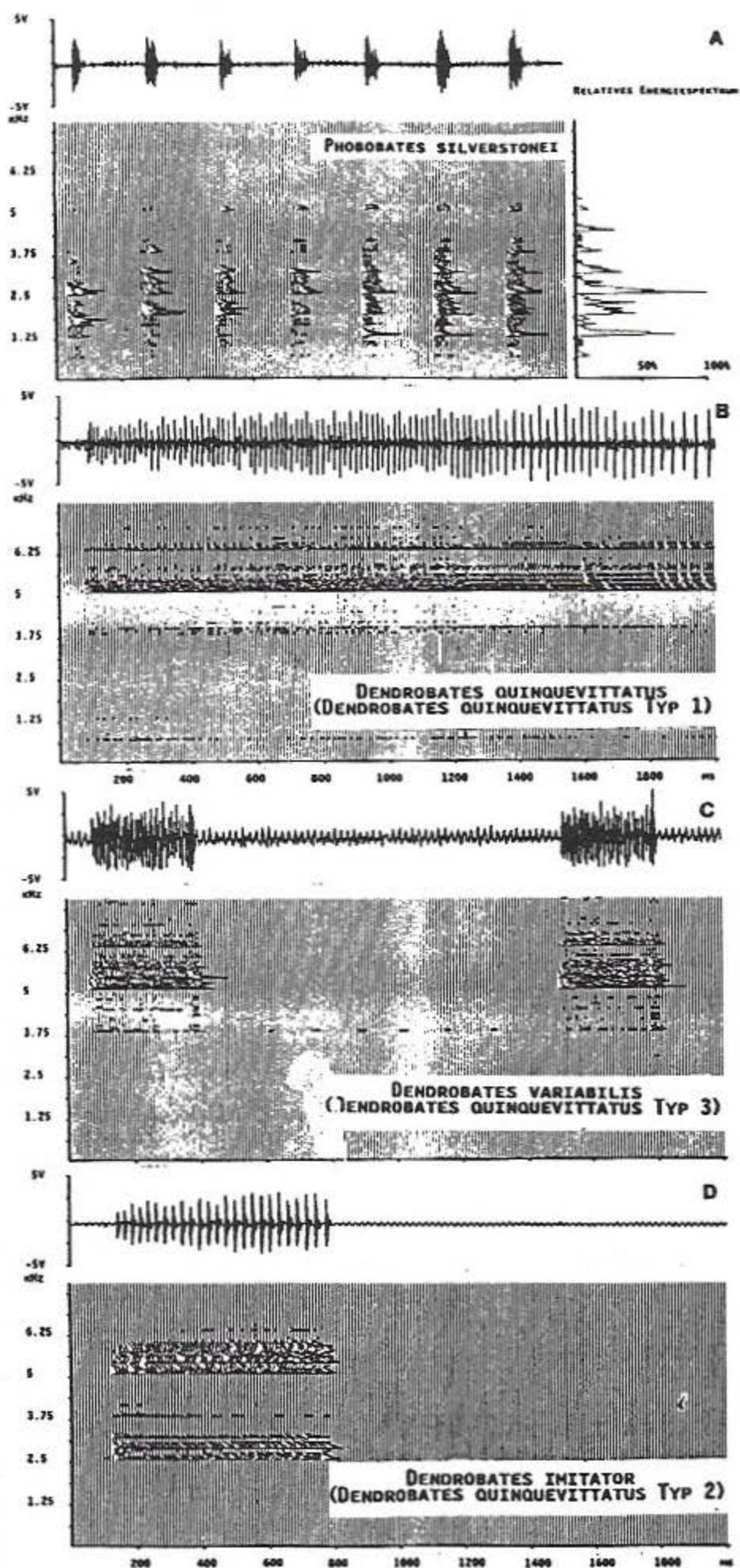


Figure 4:

Sound spectrogram (Frequency resolution = 20 Hz, time resolution virtual = 10 ms, t 24°C), corresponding oscillogram and power spectrum (summation over 13,800 ms).

A = Advertisement call of *Phobobates silverstonei*.

B = Courtship call of *D. quinquevittatus* (type 1).

C = Courtship call of *D. variabilis* (type 3).

D = Courtship call of *D. imitator* (type 2).

present to fairly well developed.

Diagnosis: *Dendrobates variabilis*, with one round black spot over its nose, differs little from *D. imitator*, which always has two black spots on the nose; although they sometimes become confluent in a variable shape. Important distinguishing traits and isolating mechanisms are: the different calls (see Table 3) and the oscillograms and sonograms (Figure 4 b,c,d). Their respective calls also distinguish *D. variabilis* from *D. quinquevittatus* (Table 3, Figure 4b,c,d). An external differential characteristic is the yellow base color of the body with two, often interrupted black stripes on the back of *D. quinquevittatus* which in some populations have coalesced into one broad black band, but which splits into a Y to form one nose spot.

3.3 Description of two new genera: *Phobobates*, for members of species group IV (*silverstonei* group) and *Allobates* for members of species group V (*femoralis* group).

Myers et al (1978) transferred 16 of the 22 species of *Phyllobates* into *Dendrobates* on the basis of toxicological characteristics. These authors also state that further efforts towards a more stable classification, especially of the genus *Dendrobates* should be made. Maxson & Myers (1985) indicate for example, that *E. espinosai* and *P. trivittatus* (the latter according to Weygoldt's (1980a) paraphyletic or even polyphyletic collective genus *Dendrobates*) do not belong in either *Dendrobates* or *Phyllobates*, and more likely than not, represent one or more different lines. Myers, in 1987, placed both *E. espinosai* and *P. trivittatus* together with 20 other *Dendrobates* species into the genus *Epipedobates*, which is characterized mainly by the longer first finger, by smaller finger discs and by the presence of teeth in many of the species.

Silverstone, and Myers et al agree (Myers et al 1978) that some morphological traits, such as teeth, cannot always be considered a clear criterion of a genus in the *Dendrobatidae*; teeth were lost in more than one evolutionary line of the family *Dendrobatidae*. Even a much more clear differential characteristic, nature and potency of skin toxins turned out to be unsatisfactory for the classification of the species, or species groups, *A. femoralis* (Myers et al, 1978). Moreover, Daly et al, (1987) found that some skin samples of *A. femoralis* contained little, or no alkaloids at all (for example, some specimens from Colombia, Ecuador, Peru and Surinam).

We use, therefore, in this article, apart from morphological and biochemical characteristics, for the first time, behavioral characteristics as a basis for a provisional classification of the *Dendrobatids* and their species groups and genera. It then

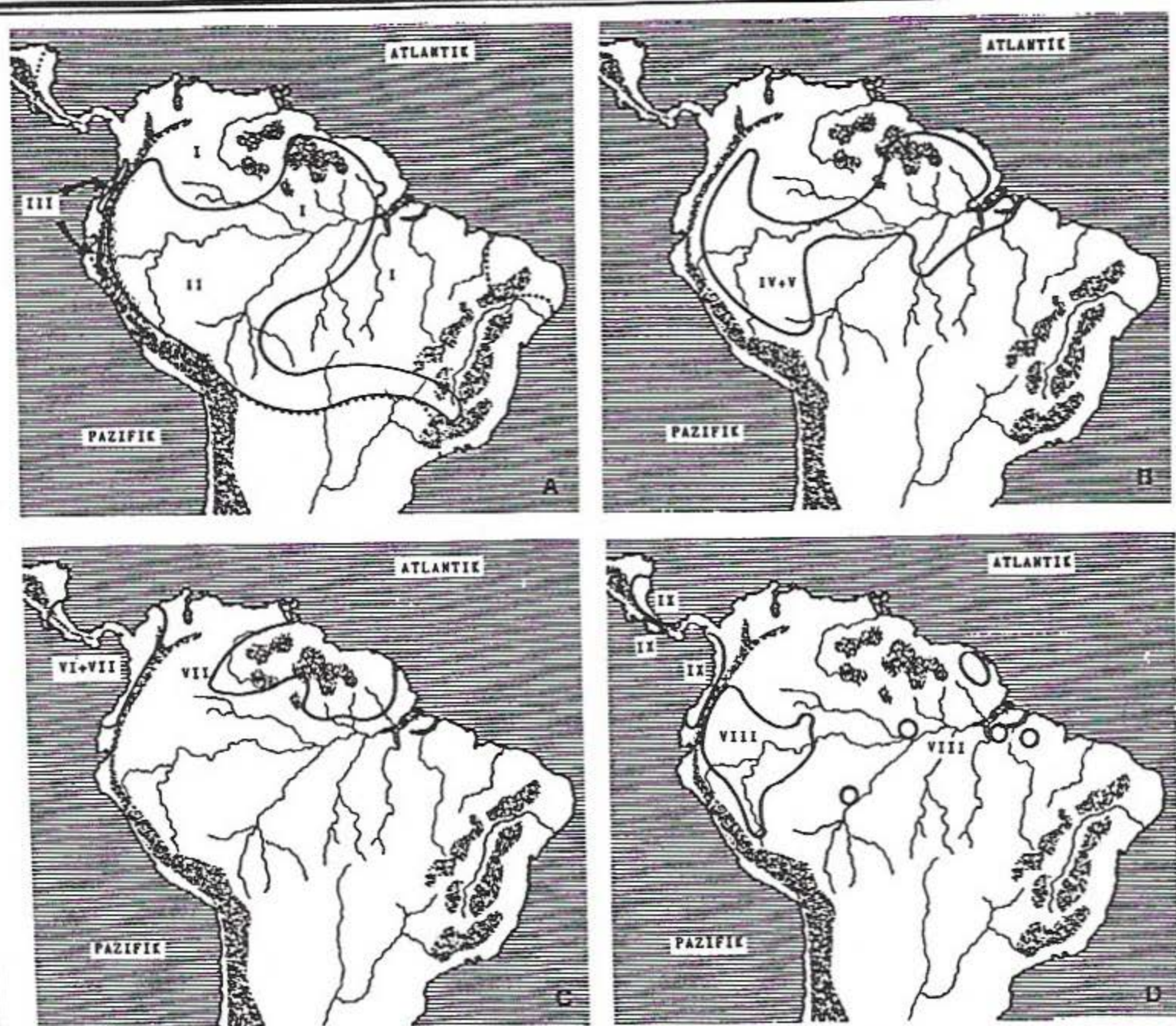


Figure 5: Geographic distribution of the species groups. A = Species groups I, II, and III. B = Species groups IV and V. C = Species groups VI and VII. D = Species groups VIII and IX.

becomes clear that groups IV (*silverstonei*) and V (*femoralis*), which are behaviorally so different from groups II (*pictus*) and III (*tricolor*), must be removed from the larger new genus *Epipedobates* and that they each deserve their own generic rank.

Phobobates [n.g. Zimmermann & Zimmermann, 1988]

Type species: *Dendrobates silverstonei* Myers & Daly, 1979.

Etymology: *Phobobates* is derived from the Greek *phobos* (fear, flight) and the Greek, *bates* (runner, walker). This name refers to the fearful behavior of members of this genus, which often flee, even when approached at a great distance.

Diagnosis: Largest members of the *Dendrobatidae* (except *D. tinctorius*). Adults 32-50 mm snout-vent length; females larger than males. Teeth present (except in *P. trivittatus*). Body color deep red, orange or green with black dorsal skin markedly bosselated. No webbing between toes. Males are territorial. During courtship, advertisement calls consist of a long sequence of single pulses (Figure 4a). Male follows female, with stroking, nodding, and body touching. Male tends and moistens the clutch, and as a rule carries all larvae at one time. (Table 2).

Phobobates differs from *Dendrobates*, *Phyllobates*, and *Allobates* by the more simple structure of its courtship (advertisement) calls, by simpler courtship and brood care behavior (without characteristics 31-49 of table 2) and by its size, (all other dendrobatids, except *D. tinctorius*, have a snout-vent length of only 16.5 - 45 mm.). *Phobobates* differs from *Epipedobates* by its more intense coloration, and the lack of many behavioral traits (characters 54-62 of table 2). However, head amplexus occurs only in species now retained in *Epipedobates*; they are significantly smaller (with snout-vent length of only 16.5 - 45mm) and have very distinct courtship calls (single pulses instead of trills).

Species included: *Dendrobates bassleri* Melin, 1941: *Dendrobates silverstonei* Myers & Daly, 1979: *Hyla trivittata* Spix, 1824.

Distribution: West, Central, and Eastern Amazonia; Peru, Ecuador, Colombia, Brazil, Guiana, and Surinam. In lowland to mountain rainforest, up to 1700 m (map Fig. 5B).

***Allobates* [n.g. Zimmermann & Zimmermann, 1988]**

Type species: *Prosterapis femoralis* Boulenger, 1884

Etymology: *Allobates* has been formed from the Greek *allos* (different, other) and *bates* (a walker). This name refers to the fact that members of this genus differ widely in behavior and attitude, and especially in toxicity and courtship calls from all other *Dendrobatids*, except *Colostethus*. The species *femoralis* comprises two bioacoustically different forms.

Diagnosis: Medium sized Dendrobatid, adults reaching 20 - 33.5 mm snout-vent length; females larger than males. Teeth present. Back black or dark brown with gold to yellow (Ecuador, Peru) or white (Brazil, Guyana) dorsolateral stripes. Ventrolateral stripes greenish bronze to white (Peru, Ecuador, Colombia) or silvery white (Brazil, Guyana). Skin of dorsum strongly granular. Toes with basal webbing. Male is territorial (Peru); Soliciting calls are a sequence of 4 (Brazil) or 3 (Peru) single pulses; in Brazilian form, larval transport by the male is only known brood care.

Allobates can be distinguished from the smaller *Epipedobates* and the larger *Phobobates*, by its less bright color, from *Phobobates*, *Phyllobates*, and *Dendrobates* by behavioral parameters (Table 2), from *Epipedobates* and *Phobobates*, *Phyllobates* and *Dendrobates* by its low or absent toxicity and by its specific display calls (Figure 2), a sequence of frequency modulated 3 or 4 pulses, which except for *Colostethus* are not known from Dendrobatids.

Referred species: *Prosterapis femoralis* Boulenger, 1884.

Distribution: Northwest, Central, and Eastern Amazonas (Ecuador, Colombia, Brazil, Guyana) and a variant form from Southwest Amazonas (Peru). Lowland rainforest to mountainous rainforest to 1750 M (Map 5B).

3.4 Origin and Distribution of Dendrobatids - a hypothesis.

To develop indications of the evolution of poison-dart frogs only the behavior of well known species has been used for the present study. Starting from the present distribution of recent species we added biogeographic, and geologic data to construct a postulated phylogenetic development.

The present distribution of Dendrobatids is characterized geomorphologically by the northern Andean chains and offshoots, the Guyana and the Brazilian shields and the Amazonas lowland in between. In the late Cretaceous there supposedly existed a land connection with Central and North America; this then disappeared in the Pliocene with the formation of the Panamanian isthmus.

The rise of the Cordilleras along the entire West Coast of South America was possible the most important event for the diversity of the Dendrobatids. It began in the Earth's middle age as a result of the continental drift, with landmasses sliding over the

oceanic crust or Nazca-plate (subduction and faulting). This went on in several phases and shifts. Only at the end of the tertiary and the beginning of the quaternary, was the last gap closed in the northern part of the long mountain chains.

The huge Amazonian lowland basin, the biogeographic province 'Hylaea' was originally connected with both the Atlantic ocean as well as the Pacific ocean via the Guayaquil depression (Fittkau 1974). Not until this last remaining gap had been closed by the rise of new mountains during the Pliocene, and after the Amazon had formed a huge inland sea, did the water masses find their way to the Atlantic through the rim of the Guyana shield. In the course of the geomorphologic modelling of this enormous region, during the tertiary, (associated with the repeated climatic shifts from moist tropical, via moderately cold and dry to the ice-ages in the Pleistocene) the larger part of South American flora and fauna developed, including the herptofauna (Haffer 1979, Savage 1973).

Within those faunistic elements evolved the Dendrobatids as a relatively young family. According to Lynch (1971, 1973) they may have shared Leptodactylid ancestors with the *Elosiinae* (*Hylodiinae*) which occur in southern South America contiguous with the *Dendrobatidae*. Both familial taxa have some morphological and behavioral traits in common; both are active by day, and some *Elosiinae* species are reported to have skin toxins as well. The first appearance of the Dendrobatids or their direct predecessors, occurred in fairly recent geological time, although authors differ in the estimates: the tertiary (Savage 1973, and Baez & Gasparil 1979), 44 million years ago (Silverstone 1975), 5 million years ago for *Phyllobates* (Maxson & Myers 1985).

According to our analysis of the behavioral parameters of different species groups we estimate that the appearance of the immediate ancestors of the present Dendrobatids followed the break in the land connection between South and Central America at the end of the Paleocene (60 million years ago), and before the rise of the northern Andean chains and their connection to Central America, and the closure of the Guayaquil pass in the Pliocene (10 million years ago).

Our premises were that:

- The present species and species groups did not descend from each other, and are neither more nor less evolved;
- The separate species groups, or their immediate predecessors, evolved more or less contemporaneously (in dimensions of geological time scale) and that

- by means of specialization they have invaded new ecological niches; a process which continues up to the present time.
- The evolution of species groups, and in part also of species, may be considered a function of biotope development. According to Savage (1982) 'the important phylogenetic factor was the vicariance effect of mountain building.'

3.4.1 Evolution of 'species group' I: *Colostethus* (Fig. 5A)

The geographical distribution of *Colostethus* corresponds approximately to that of all other Dendrobatid genera; although, in general, it is confined refuge-like to the higher altitudes. From Panama to northern Peru and eastward to the Atlantic, a large number of species in varying density inhabit the Cordilleras and their offshoots, from sea level to an elevation of about 4000 meters. On the contrary, other Dendrobatids, only seldom reach 2000 meters.

As principally montane forms, *Colostethus* probably evolved mainly during the ice-ages and interglacial periods (Edwards, 1974), thus during fairly recent geological times. For this reason we are unable also to regard them as primitive Dendrobatids, - as did Lynch (1971) and Noble (1931), nor as possible ancestral forms of other Dendrobatids. They evolved complex courtship and brood care behavior as did the majority of other Dendrobatids. It is still too early to discuss the relationships and evolutionary lines of species in this genus because detailed behavioral studies are available for only a few forms.

3.4.2 Evolution of 'species groups' II, *Epipedobates pictus*, and III, *E. tricolor* groups (Fig. 5A).

Like *Colostethus*, these two species groups differ from other Dendrobatids essentially in behavioral characters. For example, cephalic amplexus in the last phases of courtship occurs only here, and does so in all species of these groups. Between them, however, they show such slight differences that a common ancestor can be assumed. At present, both groups are separated by the insurmountable (up to 6000 meter high) Andean barrier - although distributional borders, for example in Ecuador, may be as close as 200 km to each other.

This seems to be a typical case, - after Mayr (1975) - how populations separated

from their original species by barriers, remained partially isolated for some time with limited gene flow, and where subspecies, after sufficient genetic differentiation reached a specific rank; this whole idea here applies to Dendrobatid species and species group formation. The barrier was formed by closure of the last gap in the northern Andean chain, about 10 million years ago (Fittkau, 1974) when their morphologic and essential behavioral characteristics were already well formed.

As mentioned already, it is remarkable that in our terraria we could obtain hybrids, even to the F_3 generation, of all species in the *tricolor* group, and that members of the *pictus* group also hybridized in captivity (Weygoldt, pers. communication).

For species group II, *pictus*, it is characteristic to have a very wide distribution (east Andes to the Atlantic) and to be adapted well to the still, at present, very diverse environments of the large Amazonian region. *Pictus* may actually be a complex of several species, which can be distinguished by their calls; (pers. communication Hodl).

3.4.3 Evolution of 'species groups' IV, *Phobobates silverstonei*, and V, *Allobates femoralis* (Fig. 5B) as well as 'species groups' VI, *Phyllobates terribilis* and VII *Dendrobates leucomelas* groups (Fig 5C).

Representatives of these groups live in the entire northern part of South America, from the Atlantic to the Pacific coasts, the Guyana shield, East Andean slopes and the entire Amazonas region. Despite this enormous distribution and the large number of species involved, they all share a common behavioral inventory - except for some differences in the *silverstonei* and *femoralis* groups. (Within certain species groups, hybridization in captivity is known to occur). As postulated for species groups II and III, it can also be assumed here that because of their many shared behavioral characteristics they stem from common ancestors (one ancestor for both groups IV and V, and another for VI and VII). These ancestors should be approximately as old as those for groups II and III. Furthermore, it is remarkable that members of the *Phyllobates terribilis* group (VI) and the *Dendrobates leucomelas* group (VII) advanced to Costa Rica after the formation of the Panama-isthmus during the Pliocene (Savage 1982). Also group VI, after the rise of the younger Cordilleras, the southernmost mountains of Central America, underwent a comparable evolution as that of members of groups II and III, some 2000 km to the south. The newly formed barrier permitted a separation of populations with further genetic differentiation, and speciation, as is the case with other amphibians and reptiles (Savage, 1982): On the Pacific coast, *Phyllobates vittatus*, and the Atlantic coast, *Phyllobates lugubris*.

3.4.4 Evolution of 'species groups' VIII and IX, *Dendrobates quinquevittatus* and *Dendrobates histrionicus* groups (Fig. 5D).

Members of both of these groups developed quite differently from those discussed previously. They developed new ecological niches by further specialization of their typically dendrobatid oviposition and brood care manner, not requiring the presence of ponds or streams. They live in the intermediate and high zones of tropical rain forests, where the smallest quantities of water, in leaf axils or bromeliads, are sufficient for the maintenance of their species.

Dendrobates quinquevittatus (type 1) occurs in the lowland rainforest of the Amazon, from its tributaries in Peru and Ecuador to its estuary in an islet-like distribution (see Ref. 5D). Reported localities for the sister species *D. imitator* and *D. variabilis*, are confined to small areas on the slopes of the tributaries, like those of *D. reticulatus* and *D. fantasticus*. These species, especially *D. quinquevittatus*, *D. imitator*, and *D. variabilis*, evolved new reproductive strategies because of their habitats in epiphytic biotopes of the tropical rainforests (Walter & Breckle, 1984) (Zimmermann & Zimmermann, 1982/1987). The male of *D. quinquevittatus* carries 1-2 hatched larvae on his back to waterfilled bromeliads. The female deposits additional eggs in the bromeliad leaf axils or on a leaf. The tadpoles feed on these eggs, or on hatching larvae that slide into the water; they will, however, eat vegetable matter. Only one tadpole will develop in a bromeliad leaf axil.

The female of *D. imitator* (type 2) normally deposits only one egg, after a very elaborate display, on a inclined or a vertical leaf (Fig 6). This egg is kept moist and watched continuously, and the hatching larva is transported by the male, accompanied by the female, to a water-filled leaf axil. There the female deposits her food-eggs until the tadpole metamorphoses (Kneller 1982a; Zimmermann & Zimmermann 1982a, 1983, 1984). The tadpole, however is able to feed either carnivorously or herbivorously, if maternal feeding is discontinued, as is the case with other species in this group VIII.

The most specialized, however, are members of the *histrionicus* species group (IX). These larvae, which are transported by the female singly to separate water-filled bromeliads, can only feed on unfertilized eggs (Graeff & Schulte 1980, Jungfer 1985, Weygoldt 1980b, Zimmermann & Zimmermann 1981, 1982a,b, 1986). Whenever parental care ceases, the larvae starve to death. Such a high level of specialization cannot have arisen suddenly in one step. The evolutionary roots lie in the behavior of *D. quinquevittatus* (or its ancestral forms). Here also the habitats are separated by

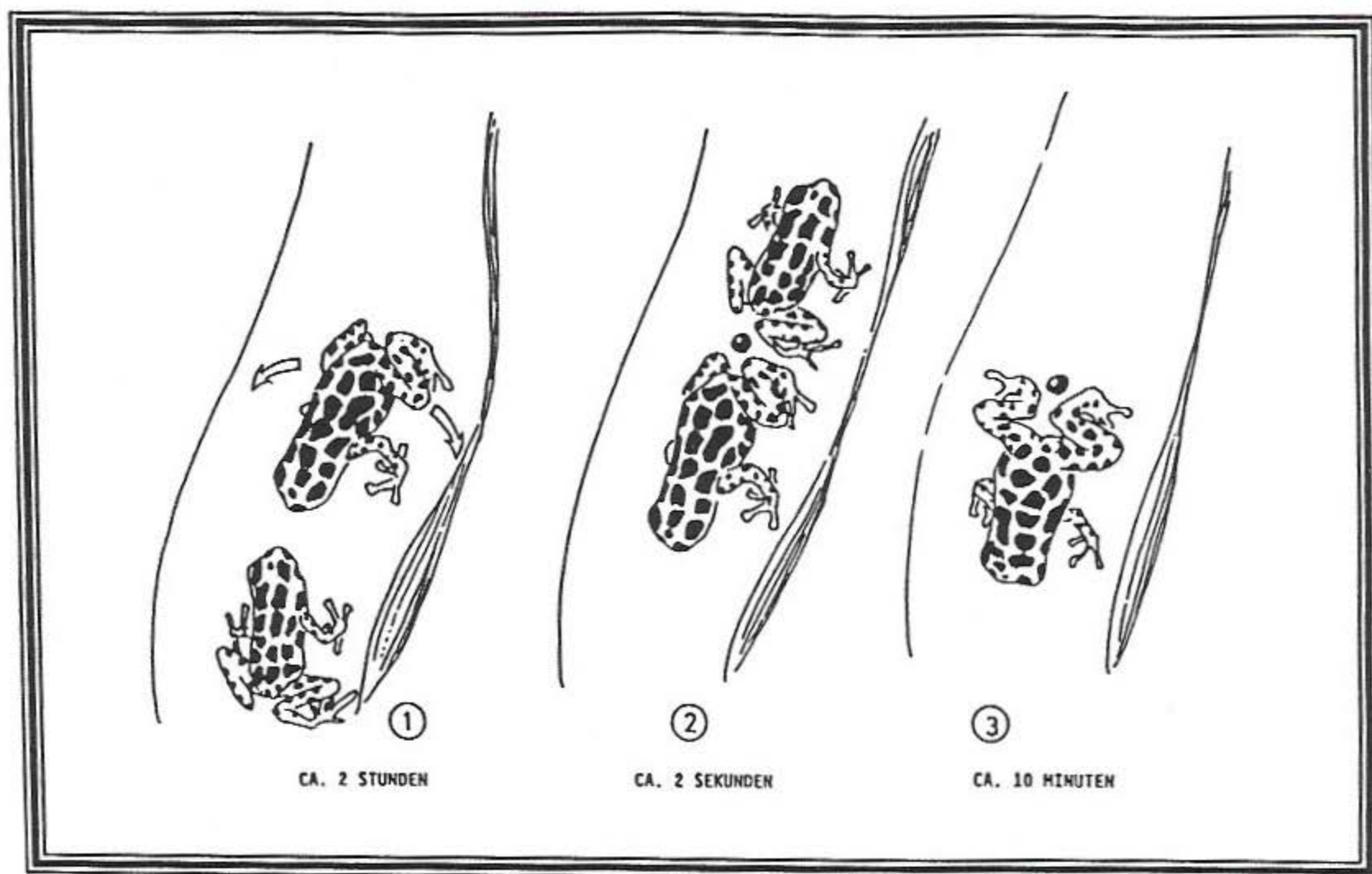


Figure 6: Courtship display and oviposition in *Dendrobates imitator* (type 2). Courtship ceremony occurs in most cases on vertical leaf sites. For about 2 hours the female moves in a half circle around the male. He remains stationary and motionless, facing the female. After many body contractions the female lays one egg. At the same moment the male jumps over the female and sits for 1-2 seconds in an anal-anal position, touching neither the female nor the egg. Then the male jumps away, but the female remains in her position for about 10 minutes (for further information see text).

only 200 km - as is the case with the *E. pictus* and *E. tricolor* groups - by the barrier at the high Andes.

Here too, the common ancestors of groups VIII and IX might have shared the same distribution before the rise of the Andes, so that both groups could develop a comparably high specialization, which was maintained in the species after the formation of the Andes. It needs to be pointed out also that some millions of years afterwards, when in the Pliocene the isthmus of Panama formed (Savage 1982), this phenomenon of speciation through montane isolation was repeated in the histrionicus group. The ancestors of this complex, which invaded Central America to Costa Rica over the new isthmus from northern South America, (like the ancestors of *P. lugubris*

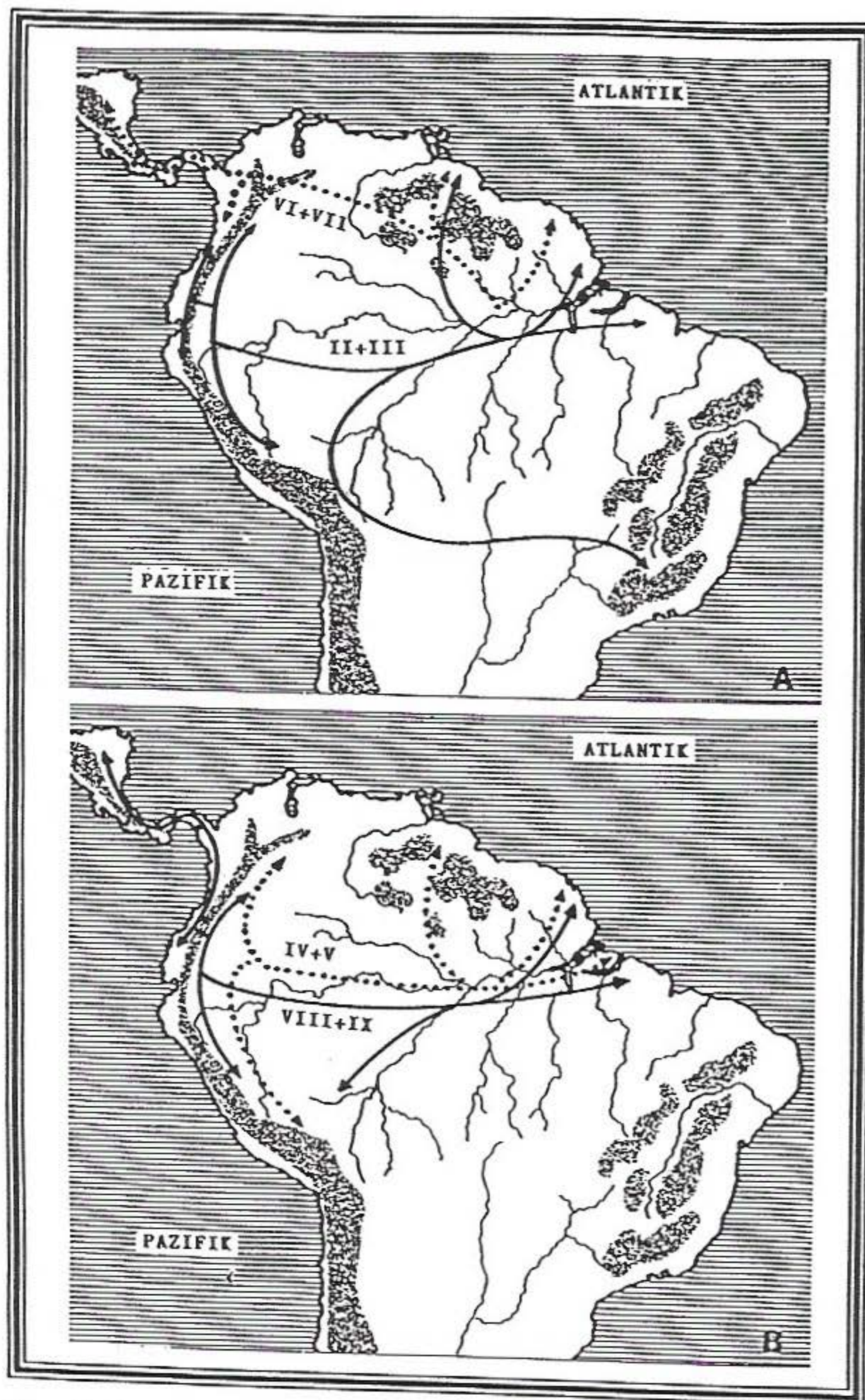


Figure 7: Dispersal of the species groups of Dendrobatid frogs from the hylaea region (Amazon Basin) into the north of South America and the south of Central America. A = Species groups II and III, VI, and VII. B = Species groups IV and V, VIII and IX.

and *P. vittatus*) were isolated by formation of mountains. They formed on the Atlantic side, *D. pumilio*, and on the Pacific side, *D. granuliferus* (Silverstone 1975, Savage 1982).

Especially remarkable seems to us the shared behavioral characteristic in the *quinguevittatus* and *histrionicus* groups: the egg feeding. This tadpole feeding behavior was transferred from the Amazonian *quinguevittatus* group to the Pacific slopes in *histrionicus* and into Central America in the complex of *D. speciosus*, *D. granuliferus*, and *D. pumilio*. According to the principle of parsimony (Ax, 1984), this indicates that the newly evolved character 'larval egg feeding' did not evolve

convergently in several sites, but originated only once in an ancestral stock (with *quinquevittatus*-like brood care) somewhere in the Hylaea-region and was then maintained after adaptive radiation and speciation in the contemporary *quinquevittatus* and *histrionicus* species groups.

3.4.5 Conclusions.

Based on the behavioral and zoogeographical findings described, we propose the following hypothesis concerning the origin and radiation of the Dendrobatid species:

- a. Even before the formation of the Andes mountains, one common ancestor existed for each of the two behaviorally related species groups in the Hylaeian biogeographic region, i.e. for groups II and III, groups IV and V, groups VI and VII, groups VIII and IX (ancestral basic stock) as well as for group I (Fig 7A & B).
- b. The evolution and diversification of the individual species groups and complexes resulted from geomorphological events; for example, the formation of mountain chains.
- c. The four basic groups mentioned in a, as well as group I (*Colostethus*), still have at least one species living exclusively in the Amazonas region. Therefore the biogeographic Amazonas region, the Hylaea, can be regarded as the origin of all five basic groups, and so of all present members of the Dendrobatids (Fig. 5A-D, 7A-B).

4. Discussion

Unlike the situation with research on speciation of birds from Amazonia, for example by Haffer (1969, 1970, 1977), there hardly has been any attention paid to the evolutionary process as it concerns the Dendrobatids. The first attempts to describe the species groups based on morphological criteria (Silverstone 1975, 1976), in many cases did not withstand subsequent careful scrutiny. Toxicological research of Myers et. al. (1978) was limited to only one group of 5 species in group VI, (*Phyllobates*). A 'preliminary report' on evolution of albumin of this group in relation to some other Dendrobatids has been published by Maxson and Myers (1985). Weygoldt (1987) summarized and analyzed one aspect of behavioral evolution, i.e. the characteristic brood care of Dendrobatids, on the basis of published evidence. Many behavioral

phenomena were discussed in detail, especially the function and possible origin of egg-feeding from a sociobiological point of view.

In the present study we have grouped 32 of the 143 known species from 7 genera (*Dendrobates*, *Minyobates*, *Phyllobates*, *Allobates*, *Phobobates*, *Epipedobates*, and *Colostethus*) into 9 species groups, mainly on the basis of behavioral characteristics; group members of which should be most closely related. This ethotaxonomic classification lays the foundation for the possibility of:

- Classifying other Dendrobatid species according to our ethological procedures.
- creating additional criteria for characterization and separation of species through methods of comparative and quantitative bioacoustics.
- Inferring the evolution of species and species groups by using the methods of phylogenetic systematics.

Evolution might not have proceeded in evolutionary jumps but through many small successive steps (Mayr, 1967). So it is likely that several intermediate forms, or behavioral connecting links, existed between the two principle categories of brood care: 1 - carrying and deposition of larvae simultaneously (in species groups I-VII) and 2 - carrying larvae and depositing them singly in bromeliads where they are fed with abortive eggs until metamorphosis (in species groups VIII and IX). We found that the barely 20 mm long frogs of the *quinquevittatus* group of species (VIII) might not only be the descendants of such a connecting link, but show amongst themselves, a range of behavioral characteristics from slightly to highly specialized behavior.

Dendrobates reticulatus, still a clumsy climber, reminds one in behavior of species in the *leucomelas* group (VII), depositing eggs on leaf litter. *D. fantasticus*, *D. quinquevittatus*, *D. imitator*, and *D. variabilis* (types 1-3) reside preferentially in the higher tree-regions, mainly on bromeliads. The reproductive behavior of *D. quinquevittatus* (type 1), which we investigated for the first time and presented here, shows that as a result of the repeated egg laying in one bromelia, together with the cannibalistic behavior of the tadpoles, only the strongest tadpole per leaf-axil is able to progress through metamorphosis.

The sister species *D. imitator* (type 2) developed a higher degree of sociability: territoriality, allegiance to locality, recognition of partners or members of a group by

means of optical, acoustic and tactile signals (like in many other Dendrobatids), and moreover, with familial brood care, with the formation of pairs, and with the cooperation of male and female in guarding and moistening the single egg they normally produce. Especially here we refer to the guiding calls and circling dance movements of the male, so that the female will be able to deposit her eggs to feed the tadpole in its bromeliad.

All this research on the complex and highly specialized courtship and brood care behavior of Dendrobatids was based, until recently, only on observations in terraria. However, by means of field studies in Ecuador we could confirm for the first time in 1984, the highest degree of specialization and the feeding of tadpoles with abortive eggs by *D. histrionicus*, (Zimmermann & Zimmermann 1985). Further observations in nature during 1986 in the Ecuadorian rainforest, along the Rio Pastaza, a large tributary of the Amazon, we confirmed our terrarium observations of the brood-care of *D. quinquevittatus*, one of the supposed intermediary forms. After identifying their calls from funnel bromeliads, many meters high, and often in treetops, we checked the same bromeliad species on cut trees on the ground in nearby clearings. On 50% of freshly cut trees we found a clutch of *D. quinquevittatus* on the leaves and at most one tadpole; moreover a few clambering adults. In older clear-cut areas we found no clutches, and no tadpoles, only dried bromeliads and, at most, one starving adult per 500 square meters of clear-cut area.

With this species one seems to be able to corroborate what Myers et. al. (1984) suspected for the recently discovered *D. arboreus* of Panama: these small species living in arboreal bromeliads adapted in the course of evolution to an epiphyte biotope with a very complex reproductive behavior (Walter & Breckle 1984).

Additional field studies of dendrobatids will be necessary, especially in the canopy of lowland rainforests, to understand the ecological causes for such a high degree of behavioral specialization of these frogs within the complex ecological mosaic of the tropical rainforest.

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RESUMEN

Por medio de 62 parámetros se describe el comportamiento de 32 especies de dendrobatidos. Utilizando similitudes de comportamientos homólogos se establecen nueve grupos. Debido a características morfológicas y etológicas discrepantes con los demás grupos, el IV y el V forman los nuevos géneros *Phobobates* y *Allobates* [n.g. H. Zimmermann & E. Zimmermann, 1988].

Los nueve grupos son: (I) el género *Colostethus*, (II) el grupo *pictus* del género *Epipedobates*, (III) el grupo *tricolor* del género *Epipedobates*, (IV) el género *Phobobates* (antes grupo *silverstonei* del género *Dendrobates*), (V) la especie *Allobates femoralis* (antes *Dendrobates femoralis*). (VI) el grupo *terribilis* del género *Phyllobates*, (VII) el grupo *leucomelas* del género *Dendrobates*, (VIII) el grupo *quinquevittatus* del

genero *Dendrobates*, (IX) el grupo *histrionicus* del genero *Dendrobates*. Se detallan estos grupos en un diagrama taxonomico.

A base de investigaciones etologicas y bioacusticas se describe la nueva especie *Dendrobates variabilis* [sp.n. H. Zimmermann & E. Zimmermann, 1988].

Relaciones parientes entre los grupos y las especies y sucesos geomorfológicos y climáticos en sus regiones de distribución permiten deducir la posible evolución y extensión de los dendrobatidos durante los periodos Terciario y Pleistoceno hasta ahora.

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Tables to follow:

Table 1

Description of 62 behavioral traits observed on dendrobatid frogs.

No.	Behavior pattern	Description	Context
1.	Pulsation of flanks and/or throat	Flanks pulsate irregularly, throat pulses in regular series	Sighting of rivals or sexual partners
2.	Toe-trembling	Middle toe moves up and down several times	As under 1, and sighting of prey
3.*	Upright posture	Bent arms are straightened, elevating anterior body	As under 1
4.	Oviposition away from water	Eggs are deposited mostly onto moist, smooth, slightly concealed sites (not into water)	Reproduction
5.	Shaking of fore or hind limbs	waving hand or foot, briefly	Courtship
6.	Female(F) follows male(M)	F follows M after courtship calls, nearby or distant	Courtship
7.	Crawling over F.	M crawls over back of F	Courtship
8.	Head-ramming	Ramming head against side of another's body	Aggression
9.	Body-pushing	Jumping at other frog, hitting body against body	Aggression
10.	Jumping against head	Frontal jumping attack	Aggression
11.	Forelimb hugging	Opponents tackle each other with arms, while standing	Aggression
12.*	Overthrowing	Throwing opponent on back or side	Aggression
13.	Jumping on the back	Jumping on back of opponent from back or side	Aggression
14.*	Clasping dorsally	Clasping waist of opponent from back	Aggression
15.	Body pressing	Pushing down rival by sitting on him	Aggression
16.*	Ducking	Subordinate ducks before dominant frog	Courtship, Submission by rival

17.	Eggs and larvae eaten by adults	Adults eat eggs or tadpoles	?
18.	Larvae carnivorous and/or herbivorous	Tadpoles eat animal or plant material	Alimentation
19.*	Larvae carried individually or in small groups	M.(or rarely F.) transport 1-10 tadpoles on its back to water	Brood Care
20.	Larvae carried in large groups	M. transports many or all tadpoles from one site to water	Brood Care
21.	Call as irregular single pulses	M. calls in irregular series of single pulses (Tonal/Harmonic)	Advertisement or Courtship
22.+	Call is a single pulse series, (retarded trill)	M. emit single pulses in regular, long intervals	Advertisement, Courtship (<u>Phobobates silverstonei</u> Fig. 4A)
23.+	Call consisting of 3 or 4 pulse series	M. emit sequence of 3-4 pulses at intervals	As in 22 (<u>Allobates femoralis</u> , Fig. 2D)
24.+	Call is a single croak	M. emit single loud croaks (noisy?) (noiselike?)	As under 22, and with aggression (<u>A.femoralis</u> , Fig. 2C).
25.+	Trills, regular single pulse series	M. emit sequences of regular pulses, trills (tonal/harmonic)	As under 22 (<u>D. leucomelas</u> , Fig. 2B)
26.	Moistening of clutch	M.(rarely F.) release water from cloaca	Brood care
27.*	F strokes male	Hand of F. strokes back of M.	Courtship
28.	Wiping ground jerkingly with hand or foot	Hand or foot wipes ground jerkingly; belly close to ground.	Courtship before oviposition
29.	"Nodding"	Jerkingly raising and lowering head in direction of partner	Courtship
30.	Body touching	F., rarely M., pushes against side of partner	Courtship before oviposition
31.*	Body-anal and/or Anal-anal-touching	Anal region of M. touches side or anal region of F.	Courtship before oviposition
32.	"Circling"	F., rarely M., circles sideways around partner	Courtship before oviposition

33.	Sloughing off rival with legs	Aggressor is pushed off back with hind legs	Aggression
34.	F puts head onto body or head of M	F. lays head on body or head of M.	Courtship
35.	F puts hand onto back of M.	F. lays hand on body of M.	Courtship
36.*	Oviposition without male	M. leaves after courtship and F. deposits eggs	Oviposition
37.	Push up with front legs	Jerkingly raising and lowering anterior body	Courtship (to impress)
38.*	Strutting	M. struts slowly, with stiff legs in front of F. or rival	Aggression, Courtship (to impress)
39.	Walking jerkily	M. moves jerkily forward	Aggression, Courtship (to impress)
40.	Raising body	M. raises body on all 4 extremities	Aggression, Courtship (to impress)
41.	Inflating body	Inflating raised body with air	Aggression, Courtship (to impress)
42.	Small number of eggs	F. deposits 1-10 eggs per clutch	-
43.	Solitary living tadpoles	Each larva lives alone in a bromelia funnel or leafaxil	-
44.	Larvae without, or with few denticles	Tadpoles without or with lip denticles	-
45.	Larvae omnivorous	Tadpoles carnivorous, herbivorous or oophagous	[Alimentation]
46.	Male defends large territory	M. defends large territory, relative to body size, against invaders	Territoriality
47.	Calls are regular croak sequences	M. emits long croaking sounds in sequence	Advertisement and Courtship calls.
48.	F feeds tadpoles with eggs	F. deposits eggs into water with tadpole	Brood care
49.	Tadpole exclusively oophagous	Tadpoles eat only food eggs, or yolk from chicken eggs as substitute	[Alimentation]

50.	Oviposition near a stream	F. deposits eggs on moist substrate near flowing water	Oviposition
51.	Calling male changes color	M. shows darker body color when calling	Aggression, Courtship
52.*	Throat display	M., F. show white, colored or dark throat	Aggression, Courtship
53.	Female defends a small territory	F. occupies small territory and chases away M. and other F.	Territoriality
54.*	"Cephalic amplexus" or mounting in species group I	M. jumps on partner and embraces her head at eye level with outsides of hands, in species group I sometimes only mounting	Courtship
55.	F. crouching under M.	F. sits opposite M. and creeps under its anterior body	Courtship
56.	Moving forward and backward in rapid sequence	Legs of M. move the curved body forward and backward	Aggression, Courtship (to impress)
57.	Guarding and defending of clutch	M., rarely F., sits near clutch, and jumps on any passing frog	Brood care
58.	Male defends small territory	M. occupies small territory and chases rivals away	Territoriality
59.	Larvae without or only few denticles but labial papillae	Tadpoles with few or no denticles, but with labial papillae	-
60.	Larvae mostly herbivorous, microphagous	Tadpoles eat mostly dust food, (windswept food) of plant origin	-
61.	Call begins as trill series and finishes as croak	M. emits single or several single pulses followed by croak	Aggression Courtship
62.	Short sequences of croaks	M. emits short croaking sequence in equal intervals	Competition, Courtship
63.	Hybridization in captivity	Hybridization for one or several generations, fertile, sometimes not	

*See Figure 1.

+See Figures 2 and 4.

CHARACTERISTICS

BEHAVIORAL SYSTEMATICS DIAGRAM

62. Short sequences of croaks
61. Trill croak combined
60. Larvae herbivorous
59. Larvae without/few denticles
58. Male defends small territory
57. Guarding clutch
56. Moving forward backward
55. F. crouching under M.
54. Cephalic amplexus or mouting
53. Female defends a small territory
52. Throat display
51. Calling male changes color
50. Oviposition near a stream
49. Tadpole exclusively oophagous
48. F feeds tadpoles with eggs
47. Calls regular croak sequences
46. Male defends large territory
45. Larvae omnivorous
44. Larvae without, few denticles
43. Solitary living tadpoles
42. Small number of eggs
41. Inflating body
40. Raising body
39. Walking jerkily
38. Strutting
37. Push up with front legs
36. Oviposition without male
35. F puts hand onto M
34. F puts head onto M
33. Sloughing off rival
32. Circling
31. Body-anal Anal-anal-touching
30. Body touching
29. Nodding
28. Wiping ground jerkily
27. F strokes M
26. Moistening of clutch
25. Regular single pulse, trill
24. Call is a single croak
23. 3 or 4 pulse series
22. Single pulse series
21. Call as irregular single pulses
20. Larvae carried in large groups
19. Larvae carried individually
18. Larvae carnivorous herbivorous
17. Eggs and larvae eaten by adults
16. Ducking
15. Body pressing
14. Grasping dorsally
13. Jumping on the back
12. Overthrowing
11. Forelimb hugging
10. Jumping against head
9. Body-pushing
8. Head-ramming
7. Crawling over F.
6. Female(F) follows male(M)
5. Shaking of limbs
4. Oviposition away from water
3. Upright posture
2. Toe-trembling
1. Pulsation of flanks throat

Hybridisation (so far):

F=Fertile N=Not Fertile

Species Groups

BEHAVIOR PATTERNS

Ascertained

Not pronounced or

probable

Unknown



TABLE 2:

Etho-Taxonomic Diagram: Different degrees of similarities in specific behavior characteristics are used to indicate relationships among species and species groups.

Call Characteristics	Type 1 One-Pointer <i>D. quinquevitt.</i> (Yellow)	Type 2 Two-Pointer <i>D. imitator</i> (Green)	Type 3 One-Pointer <i>D. variabilis</i> (Green)
Frequency range (kHz)	2.5-8.46	2.5-6.9	2.5-8.7
Dominant frequency (kHz)	5.1-5.4	5.1-6.9	5.2-6.6
Formant (kHz), \bar{x} +SD	5.28+0	5.67+0.78	5.64+0.33
Pulse duration	Short	Long	Short
Pulse sequence	Irregular, mostly recognizable single pulse	Regular, clearly recognizable single pulse	Irregular, partly recognizable, partly fused single pulse
Pulse rate(n/sec)	30-130	35-50	80-115
Call duration \bar{x} +SD Range (ms)	1019.6+513 337-2031	581+139 341-1098	216+78 196-502
Intercall Interval \bar{x} +SD, Range (ms)	1896+1356 601-5601	2153+840 1160-3662	982+206 643-1372
Call sequence	Very irregular	mostly regular	regular
Sound pressure level (dB)	max. 65	max. 84	max. 60
Miscellaneous			Intercall interval with 4-7 soft single pulses
No. of analyzed calls	29	57	60

TABLE 3:

Physical characteristics of calls in the *Dendrobates quinquevittatus* complex (mean \bar{x} , \pm SD, $t = 24^{\circ}\text{C}$).

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